Annals of the Entomological Society of America, 113(1), 2020, 30–39
doi: 10.1093/aesa/saz052
Advance Access Publication Date: 18 October 2019
Research

Research

Description, Biology, and Impact of the Fruit-Feeding Moth, *Mompha luteofascia* sp. n. (Lepidoptera: Momphidae), on *Miconia calvescens* (Melastomataceae) in Costa Rica

Manuel Antonio Alfaro-Alpízar,[1] Sjaak (J. C.) Koster,[2] M. Tracy Johnson,[3] and Francisco Rubén Badenes-Pérez[4,5,]

[1]Escuela de Biología, Universidad de Costa Rica, San Pedro de Montes de Oca, San Jose, Costa Rica, [2]Naturalis Biodiversity Center, 2300 Leiden, The Netherlands, [3]Institute of Pacific Islands Forestry, Pacific Southwest Research Station, USDA Forest Service, Volcano, HI 96785, [4]Instituto de Ciencias Agrarias (CSIC), 28006 Madrid, Spain, and [5]Corresponding author, e-mail: fr.badenes@csic.es

Subject Editor: Hector Carcamo

Received 1 July 2019; Editorial decision 5 September 2019

Abstract

Fruits of *Miconia calvescens* DC. (Melastomataceae) were dissected to study insect frugivory in this plant in its native habitat in Costa Rica. Larvae of an unknown *Mompha* species (Lepidoptera: Momphidae), *Anthonomus monostigma* Champion (Coleoptera: Curculionidae), and unidentified Diptera and Hymenoptera were found in *M. calvescens* fruits. The *Mompha* species, described here as new as *Mompha luteofascia* Koster & Badenes-Pérez, was the most abundant insect frugivore in *M. calvescens*, infesting up to 38.1% of the fruits sampled. Feeding damage by *M. luteofascia* was positively correlated with fruit maturity, and resulted in significantly reduced numbers of seeds and rates of seed germination. *Miconia calvescens* fruits with medium damage (50–75% of the pulp missing) and high damage (75–100% of the pulp missing) had an average of 96 and 99 seeds, respectively, whereas undamaged fruits contained an average of 127 seeds per fruit. In fruits with medium and high fruit damage, only 1.9 and 0.1% of the seeds germinated, respectively, whereas 34.8% of the seeds germinated in undamaged fruits. *Mompha luteofascia* developed through three instars, as determined from measurement of head capsules. Larvae usually fed as one individual per each fruit attacked, exiting fruit to pupate in foliage or litter. Parasitism of *M. luteofascia* larvae was substantial, averaging 64 and 38% at the two study sites. Although host specificity of *M. luteofascia* has not been evaluated, the significant reductions in seed numbers and seed germination caused by its larvae indicate that this species deserves further assessment as a potential biological control agent of *M. calvescens*.

Key words: biological control of weed, frugivory, seed germination

The velvet tree, *Miconia calvescens* DC. (Melastomataceae), is a small tree native to Central and South America that is an invasive species in Australia, Hawaii, Tahiti, and other Pacific islands (Meyer and Florence 1996, Medeiros et al. 1997, Le Roux et al. 2008, Hardesty et al. 2011). It is considered a serious threat to native ecosystems on islands where it has invaded or might invade (González-Muñoz et al. 2015, Libeau et al. 2019). In Tahiti, *M. calvescens* has displaced over 65% of the native forest, threatening almost 100 native plant species (Meyer and Florence 1996). Biological control is considered an essential tool for long-term management of *M. calvescens* (Denslow and Johnson 2006, Johnson 2010, Meyer and Fourdrigniez 2011).

The success of *M. calvescens* as an invasive plant is partly due to its prolific reproduction, with one mature tree flowering up to three times per year and bearing up to 220 inflorescences that can produce more than 200 fruits each, with up to 200 seeds per fruit (Medeiros et al. 1997, Meyer 1998, Badenes-Pérez and Johnson 2007b). In its native habitat, inflorescences of *M. calvescens* are attacked by a variety of insect herbivores (Badenes-Pérez and Johnson 2007b, Badenes-Pérez et al. 2010, Chacón-Madrigal et al. 2012, Morais et al. 2012, Zaldívar-Riverón et al. 2018). During field surveys conducted to assess prospective biological control agents of *M. calvescens*, we found larvae of an unknown *Mompha* species (Lepidoptera: Momphidae) feeding on *M. calvescens* fruits. This fruit feeder was selected for detailed evaluation, along with other natural enemies including shoot-tip feeders, stem borers, defoliators, and gall formers, with the long-term goal of developing a suite of

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Version of Record, first published online October 18, 2019 with fixed content and layout in compliance with Art. 8.1.3.2 ICZN.

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biocontrol agents that damage *M. calvescens* in multiple ways to lower its overall fitness (Johnson 2010).

The family Momphidae (Lepidoptera) is in the superfamily Gelechioidea, the largest superfamily of microlepidopterans (Powell 1980). So far, approximately 115 species have been described in this family (van Nieukerken et al. 2011). Most of the species described in the family Momphidae are Holarctic (i.e., found in the northern hemisphere), and within this family that contains six subgenera, *Mompha* includes the highest number of species (Koster and Sinev 2003, Heppner 2005, van Nieukerken et al. 2011). Approximately 40 of the described *Mompha* spp. are in North America and 37 species of the family Momphidae are known from the Neotropical Region, where several dozen species of Momphidae are waiting for description (S.(J.C.)K., personal comment; Dickerson and Weiss 1920, Scoble 1992, Graham 1995, Koster and Sinev 2003, Wagner et al. 2004, Koster and Sammut 2006, Emery et al. 2009, Powell and Opler 2009).

Mompha adults are small moths, typically with scales developing as hairs in their hindwings and with long antennae that are placed along their body when moths are at rest (Dickerson and Weiss 1920, Heppner 2005). Larvae are usually white and often change color to yellow or red when they reach the final instar (Dickerson and Weiss 1920, Burkhart 1988, Wagner et al. 2004). Larvae of *Mompha* spp. can be leaf miners, stem miners, fruit and pod feeders, gall inducers, or live between spun leaves (Powell 1980, Graham 1995, Koster and Sinev 2003, Wagner et al. 2004, Heppner 2005). *Mompha* spp. tend to be highly host specific, which increases their utility as potential biological control agents of invasive plants (Bradley et al. 1973, Culliney et al. 2003). Most reports of host plants for *Mompha* spp. are in Onagraceae, with *Oenothera* and *Epilobium* being the genera most studied as host plants (Dickerson and Weiss 1920, Powell 1980, Wagner et al. 2004, Heppner 2005, Powell and Opler 2009, Looney et al. 2012, Eiseman 2016). *Mompha* spp. have also been reported feeding on Cistaceae, Fabaceae, Fagaceae, Lythraceae, and Rubiaceae (Powell 1980, Graham 1995, Wagner et al. 2004, White et al. 2016). *Mompha trithalama* Meyrick, a fruit feeder specialized on *Clidemia hirta* (L.) D. Don (Melastomataceae), was introduced to Hawaii for biological control (Burkhart 1986, 1988; Anonymous 1987; Nakahara et al. 1992; Conant 2002).

The main objectives of this research were to describe and study the biology of *M. luteofascia* Koster & Badenes-Pérez on *M. calvescens* in its native habitat in Costa Rica; to assess the incidence of *M. luteofascia* compared with other herbivores; and to determine the effect that feeding by *M. luteofascia* larvae had on *M. calvescens* seed set and seed germination. We hypothesize that feeding by *M. luteofascia* larvae could reduce seed set and seed germination in *M. calvescens* fruits.

Materials and Methods

The presence of herbivores feeding on *M. calvescens* fruits was investigated in two field sites in Costa Rica, Cariblanco (10°18′59″N and 84°11′00″W, 986 m above sea level) and Vereh (09°40′00″N and 83°31′40″W, 1,200 m above sea level), which were approximately 60 km apart. To increase the abundance of this normally uncommon plant, 200 *M. calvescens* plants were planted between 2003 and 2005 in a cleared plot of approximately 1,000 m^2 in Cariblanco, whereas 50 *M. calvescens* plants were planted over the same period in a 300 m^2 plot in Vereh. At the time of this study, plants ranged from immature trees about 1 m high to reproductively mature trees up to about 4 m high. In these sites, located in Cariblanco and Vereh, there were also natural populations of *M. calvescens*, consisting of 10–20 mature trees ranging from 3 to 8 m in height within several hectares of lightly disturbed native secondary rainforest. At the Cariblanco site, conditions were very wet (>7,000 mm of annual rainfall) with no dry season. The Vereh site was less wet (approximately 3,000-mm annual rainfall) with a 1- to 2-mo dry season. At an additional planted site in Sabanilla de Montes de Oca (09°56′48″N and 84°02′45″W, 1,200 m above sea level), located more than 60 km from known natural populations of *M. calvescens*, we did not find *M. luteofascia*.

Laboratory studies were conducted at the Department of Biology of the University of Costa Rica in San Pedro de Montes de Oca. During the period when insects were being reared in the laboratory conditions, there were approximately 11-12:13-12 (L:D), with temperature and relative humidity of 22 ± 3°C, and 68 ± 5%, respectively. Voucher specimens of *M. luteofascia* were deposited in the Zoology Museum of the Department of Biology at the University of Costa Rica; at Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas (CSIC), Madrid, Spain, and at Naturalis Biodiversity Center, National Museum of Natural History (RMNH, Rijksmuseum voor Natuurlijke Historie), former Leiden Zoology collections, Leiden, The Netherlands.

Description and Biology of *M. luteofascia*

In total, 16 adult insects collected in Cariblanco and Vereh were used for the description of the species. To determine the morphology of the species, genitalia were dissected following previously published methodology (Robinson 1976, Brown 1997). For the slides of the male genitalia, phenosafranin was used for staining. Chlorazol black was used to stain the unsclerotized parts of the female genitalia. To determine the number of instars of *M. luteofascia*, a total of 274 larvae were collected from the field sites in Cariblanco and Vereh and placed in 70% ethanol. Head capsule width, measured as the distance between genae, was recorded for each larva using a stereomicroscope with a micrometer (Dyar 1890). In total, 32 pupae of *M. luteofascia* were placed individually in 50-ml glass flasks and followed to adult emergence. To study the parasitism of *M. luteofascia*, infructescences with mature fruit were collected at Cariblanco and Vereh and brought to the laboratory to determine rates of parasitism of *M. luteofascia* larvae. Approximately three infructescences, each from a separate tree, were collected at each site across several dates in November and December 2006. From each infructescence, approximately 5–20 late-instar larvae were removed and placed in a 100-ml glass jar with 1.5 cm of moist vermiculite at the bottom for pupation. Jars with pupae were checked every 2 d for emergence of either parasitoids or *M. luteofascia* adults.

Herbivore Abundance and Damage in *M. calvescens* Fruits

Infructescences were collected from Cariblanco and Vereh to determine the number of fruits with larvae of different insect herbivores and the damage present per fruit. Sampling was conducted June through August 2006 in Cariblanco and January through March 2007 in Cariblanco and Vereh. In total, 3–15 infructescences from a total of 3–10 different trees were collected each month per site and 56–150 randomly selected fruits were dissected from each infructescence. The maturity of each fruit was classified visually as green, greenish pink, pink, or purple. Upon dissection, herbivores were identified, and fruit damage was classified according to six levels of damage: 0 (no damage), 5, 25, 50, 75, or 100% damage (i.e., pulp missing).

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Impact of *M. luteofascia* on Seed Numbers and Seed Germination

To quantify the effect of *M. luteofascia* on fruit seed number and germination, the number of seeds was determined in a total of 80 mature fruits. Fruits were randomly selected from infested infructescences collected from three different plants in Vereh in March 2007. Upon dissection, each fruit was classified as undamaged ($n = 63$); containing one *M. luteofascia* larva and having 50–75% fruit damage ($n = 5$); or containing one *M. luteofascia* larva and having 75–100% fruit damage ($n = 12$). Sampling was directed toward fruits from which fully fed larvae had already emerged, to quantify maximal expected impacts of *M. luteofascia* on a per fruit basis. For this particular part of the study, all fruits sampled showed more than 50% damage. After counting the number of seeds per fruit, seeds of each fruit were placed on wet filter paper in a glass petri dish (15 cm diameter). Seeds were moistened every 3 d, and germination was recorded at 40, 60, 90, and 120 d. Germinated seeds were removed at each time step.

Statistical Analysis

A cluster analysis was performed with the capsule width data using the K-Means Cluster analysis of SPSS version 25 to determine the total number of larval instars in *M. luteofascia*. The instar classification based on the cluster analysis was followed by a one-way analysis of variance (ANOVA) and Tamhane's T2 test ($P \leq 0.05$) to separate means. This analysis has been previously used to determine larval instars in another lepidopteran species (Castillo et al. 2014). Differences in the percentage of fruits from the total number of fruits sampled that were undamaged or damaged by a particular herbivore were analyzed using a one-tailed two-sample test of proportions ($P \leq 0.05$) with Stata version 15.1. Differences in fruit damage (among months within the same site and between sites) were analyzed by Kruskal–Wallis and Mann–Whitney *U* tests with SPSS version 25. Correlations between fruit damage and fruit maturity were performed using one-tailed Spearman's correlation with SPSS. Kruskal–Wallis tests were also used to compare differences in fruit damage among the different levels of fruit maturity. Data comparing seed number and percentage of seed germination according to fruit damage were analyzed with Kruskal–Wallis and Mann–Whitney *U* tests with SPSS.

Nomenclature

This article and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:A3900AF4-46DD-4FA2-967F-CF7A1D001F4B

Results

Description and Biology of *M. luteofascia*

(Zoobank LSID: urn:lsid:zoobank.org:act:0FC21AC0-DA33-4E21-86B1-A33D8F0228FC)

Type Material

Holotype ♂, Costa Rica: Cartago, Turrialba, Tayutic-Vereh, 09 29 45N 83 38 45W, 1,200 msnm, 5 January 2007, Col[lection] Manuel Ant. Alfaro Alpizar, Col[lected from] de frutos *Miconia calvescens*; genitalia slide JCK 6908 (CSIC). Paratypes 8♂, 6♀, 1 gender unknown. 2♂, 1♀, 1 gender unknown, Costa Rica: same location as holotype, 2.i.2006; genitalia slide JCK 6907. 3♂: Costa Rica: same location as holotype; genitalia slide JCK 6531 (RMNH). 2♂, 3♀: Costa Rica: Alajuela, Sarapiquí, Cariblanco, 10 18 59N 84 11 00W, 986 msnm, 27 July 2006, Col. Manuel Ant. Alfaro Alpizar, Col. de frutos *Miconia calvescens*; genitalia slide JCK 6532 (RMNH). 1♂, 2♀: Costa Rica: same location, 9.xii.2006; genitalia slide JCK 8693 (CSIC).

Diagnosis

The dark brown forewing with the bent yellow fascia at one-third is characteristic. In the male genitalia, *M. luteofascia* resembles *Mompha trithalama* by the uncus split into two brachia, but can be distinguished from this species by the broader cucullus with rounded tip and by the longer sacculus with a bend and pointed tip. In the female genitalia, it can be distinguished by the very long and distally widening lobes of the lamella postvaginalis in combination with the small corpus bursae with a small appendix bursae.

Description

Male (Fig. 1), Female. Forewing length: 2.5–3 mm. *Head*: frons shining silver metallic with greenish and reddish reflections, vertex shining ochreous-white with reddish gloss and some brown irroration on top, neck-tufts and collar shining dark brownish gray; labial palpus white, first segment very short; second segment one-third longer than third, apical two-thirds roughly scaled and dark gray irrorated ventrally, apically white; third segment with dark gray basal, medial and subapical rings; scape dorsally dark brownish gray with paler irroration, ventrally shining ochreous-white, no pectines; flagellum shining dark gray, indistinctly darker annulated, ventrally paler. *Thorax and tegula*e dark brownish gray. *Legs*: shining dark gray with paler irroration, femur hindleg shining creamy white; foreleg with tarsal segment five white; tibia midleg with white medial and apical rings, tarsal segments one, two, and four with white apical rings, segment five white; tibia hindleg with white apical ring; tarsal segments as midleg; spurs dark gray, apically white. *Forewing* shining dark grayish brown with paler irroration; at one-third a broad and bend, outward oblique, yellow fascia, paler at sides and edged blackish brown; three yellowish brown spots, first spot subcostal at two-thirds, paler toward costa and lined blackish brown, second spot below first spot, similarly colored, much smaller and just above fold, third spot at apex, paler toward costa, strongly mixed brownish gray toward dorsum, in middle with narrow blackish brown streak toward apex; two blackish brown tufts of raised scales on dorsum, first tuft at one-half, second tuft at three-fourths and about half the size of first tuft; cilia gray around apex, strongly irrorated dark gray, brownish gray toward dorsum, three ciliary lines around apex, the inner two complete, the outer only at costa. *Hindwing* shining brownish gray, cilia brownish gray. *Underside*: forewing shining dark grayish brown, dark ciliary lines distinctly visible; hindwing shining brownish gray. *Abdomen* dorsally shining dark grayish brown, ventrally shining gray with reddish gloss, segments shining pale gray banded posteriorly; anal tuft dorsally grayish brown, ventrally ochreous-white. *Female*: flagellum of antenna thinner and less flattened, annulations more distinct.

Male Genitalia. Uncus with two brachia, long, slightly bend and widening distally, beyond base large inward tooth on each brachium, apex wide and flat, about as long as tegumen (Fig. 2a and b). Tegumen broad and elongated, height larger than width. Transtilla large, band-shaped, weakly sclerotized. Cucullus short, widening from base and beyond one-half narrowing distally, apex rounded. Sacculus slightly shorter than cucullus, elongated triangular, apex bend and pointed. Vinculum elongated. Phallus (Fig. 2b) short and

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Fig. 1. *Mompha luteofascia*, male habitus. Watercolor J. C. Koster.

broad, vesica with two long and parallel bundles of numerous small cornuti and many tiny spicules, juxta lobes long and ear-shaped.

Female Genitalia. Papillae anales small and narrow, apophyses posteriores one-third longer than length of apophyses anteriores (Fig. 2c). Tergite 8 convex. Antrum very wide and deep, vase-shaped, anteriorly with sclerotized ring. Lamella postvaginalis as two large, broad, and somewhat slant lobes, covered with spicules and long setae; lamella antevaginalis absent. Colliculum absent. Ductus bursae from antrum rather wide till one-third of length, remaining two-thirds to corpus bursae narrow, about three times as long as length of corpus bursae. Ductus seminalis very narrow, starting in middle of wider part of ductus bursae. Corpus bursae small, circular with small appendix bursae, two narrow sickle-shaped signa.

Biology

Miconia calvescens fruits infested by *M. luteofascia* contained typically only one larva and have a little mark, visible with the naked eye, which indicates the entry point of a larva (Fig. 3a and b). The frequency distribution of head capsule widths showed three separate peaks (Fig. 4). The instar classification based on cluster analysis, followed by an ANOVA, and Tamhane's T2 test, confirmed the significance of three larval instars in *M. luteofascia* (F = 1067.73; df = 2, 271; $P \leq 0.001$). Head capsule widths (mean ± SE) were 0.15 ± 0.01, 0.28 ± 0.00, and 0.44 ± 0.02 mm for the first, second, and third instars, respectively. Larvae are white in the early instars, turning orange-red when they reach the last instar (Fig. 5a). After feeding inside the fruit throughout their development, last instars exit the fruit to pupate, spinning a yellowish-light brown cocoon (Fig. 5b). In the laboratory, insects remained as pupae for 25.0 ± 0.4 d (mean ± SE), before emerging as adults.

Parasitism

Three hymenopteran parasitoid species were reared from field-collected *M. luteofascia*: an undetermined Campopleginae (Ichneumonidae), *Bracon* sp. (Braconidae), and *Chelonus* sp. (Braconidae). Percent parasitism of late-instar larvae (mean ± SE) was 63.9 ± 14.9% at Cariblanco and 37.9 ± 8.7% at Vereh.

Distribution

So far, *M. luteofascia* has only been found in Costa Rica. Examination of *M. calvescens* fruits in three different locations in Brazil did not indicate the presence of *Mompha* spp. there (Badenes-Pérez and Johnson 2007b, Morais et al. 2012).

Etymology

Named for the broad yellow fascia on the forewing. To be treated as a noun in apposition. For taxonomic purposes, Sjaak (J. C.) Koster is to be considered the author of the name *M. luteofascia*, of which Francisco Rubén Badenes-Pérez is coauthor.

Remarks

In the genitalia slide of the holotype JCK 6908, the two long and ear-shaped juxta lobes on the phallus overlap each other. For a better representation of the phallus with the juxta lobes, the phallus in the male genitalia of genitalia slide JCK 8693 is used to give a clearer picture of these parts.

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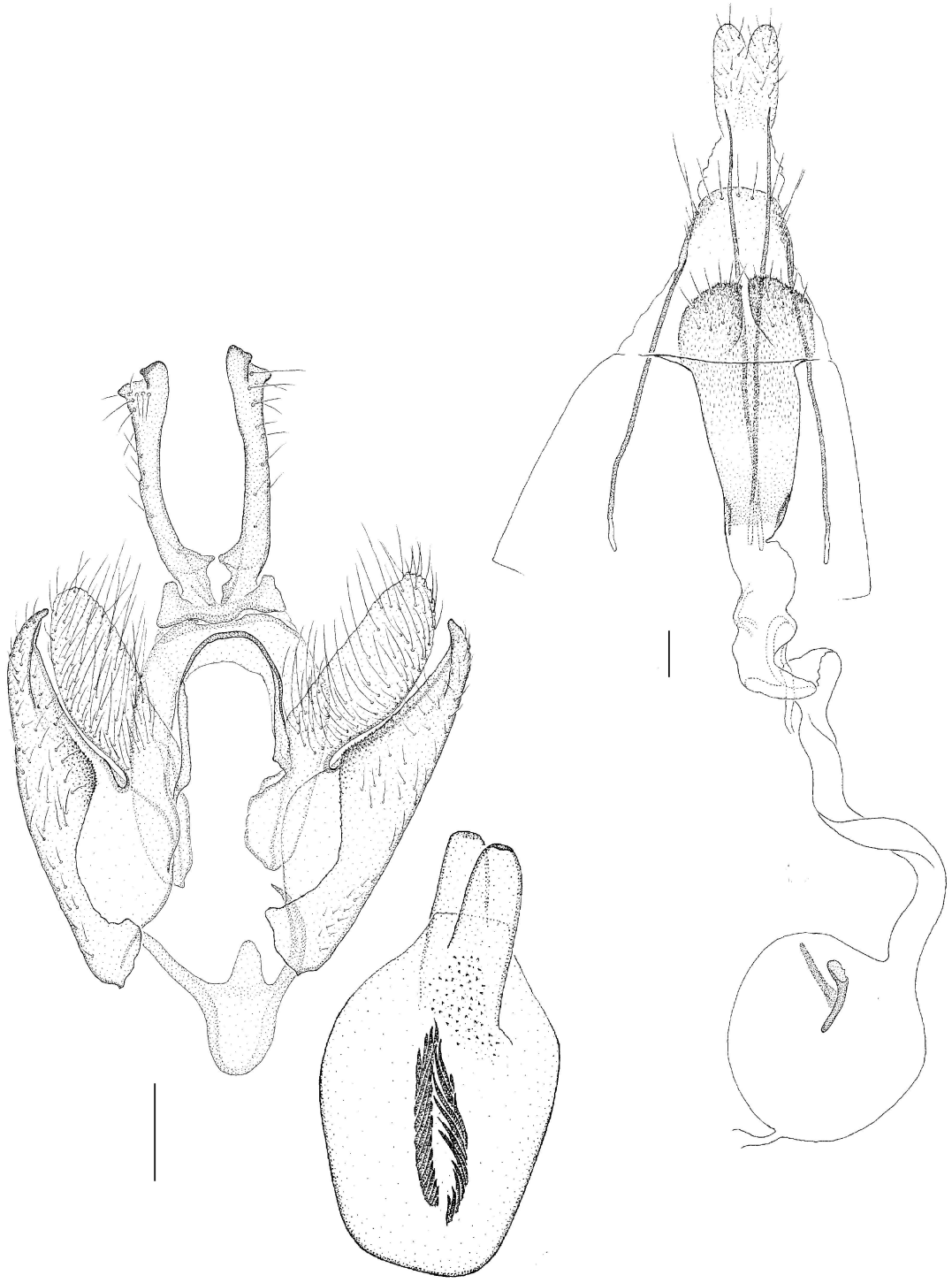

Fig. 2. *Mompha luteofascia*, male and female genitalia. Male genitalia, ventral aspect without phallus, genitalia slide JCK 6908 (holotype) (a). Phallus, ventral aspect, genitalia slide JCK 8693 (b). Female genitalia, ventral aspect, genitalia slide JCK 6907 (c). Scale bars 0.1 mm. Drawings by J. C. Koster.

Herbivore Abundance and Damage in *M. calvescens* Fruits

At Cariblanco, the most common herbivore in fruits was *M. luteofascia*, followed by Hymenopteran and Dipteran larvae ($P \leq 0.05$; Table 1; Supp Tables S1 and S2 [online only]). In Vereh, the most common herbivore in *M. calvescens* fruits was also *M. luteofascia*, followed by the fruit borer weevil *Anthonomus monostigma* Champion (Coleoptera: Curculionidae), Dipteran, and Hymenopteran larvae ($P \leq 0.05$; Table 1; Supp Tables S1 and S2 [online only]). In both Cariblanco and Vereh, fruit damage in fruits with herbivores was highest for *M. luteofascia* ($P \leq 0.05$; Table 1; Supp Tables S1 and S2 [online only]). The percentage of fruits affected by *M. luteofascia* was higher in Cariblanco than in Vereh (Tables 1; Supp Table S3 [online only]).

At both Cariblanco and Vereh, damage caused by *M. luteofascia* varied with date and damage per fruit was correlated with fruit maturity ($P \leq 0.05$; Supp Tables S1 and S4–S8 [online only]; Fig. 6). At Vereh, damage by *A. monostigma* was also affected by date and fruit

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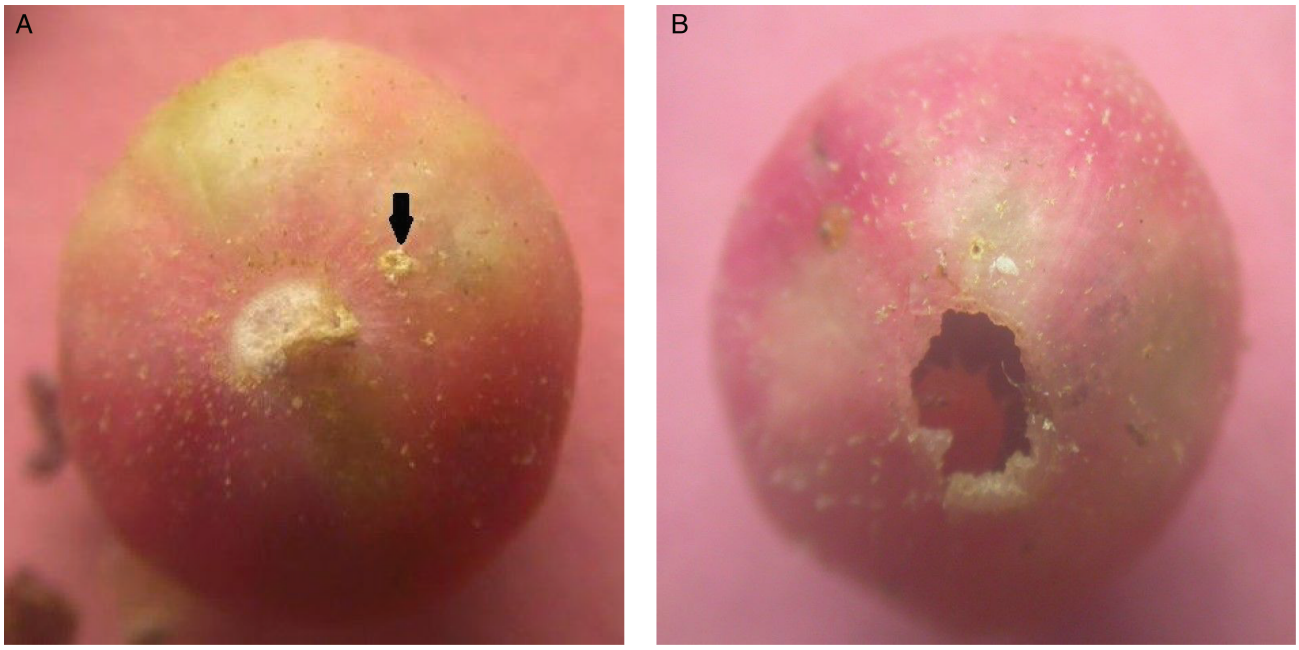

Fig. 3. Mark visible outside *Miconia calvescens* fruit indicating where *Mompha luteofascia* entered the fruit (a) and late-instar larva inside the fruit (b). Mature fruits typically have a diameter of approximately 5–7 mm (Badenes-Pérez and Johnson 2007b). Photographs by M. A. Alfaro-Alpízar.

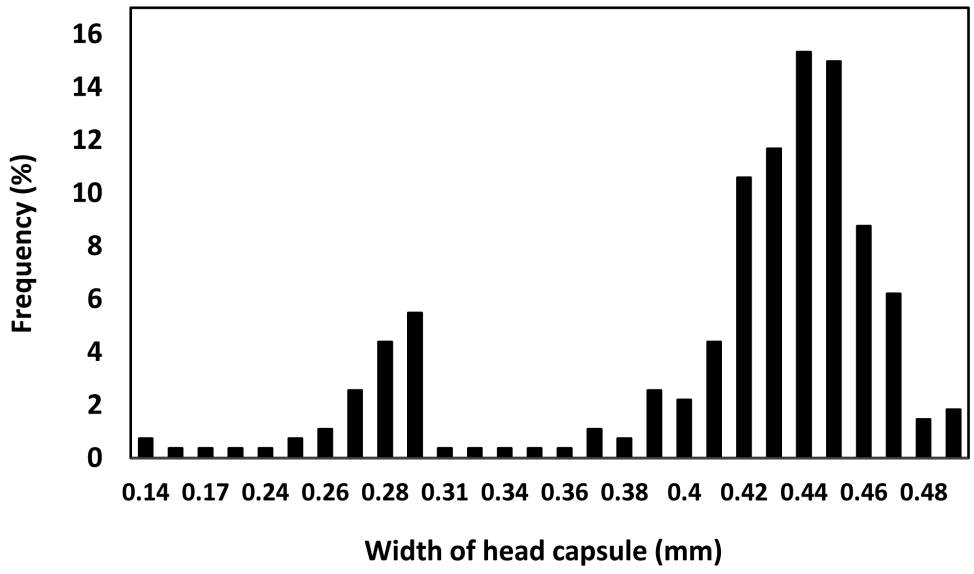

Fig. 4. Frequency (%) of head capsule widths of field-collected *Mompha* sp. larvae (n = 274).

maturity ($P \leq 0.005$), but the correlation with fruit maturity was not significant ($P = 0.060$; Supp Tables S1 and S4–S8 [online only]). At both Cariblanco and Vereh, the effects of date and fruit maturity on the damage associated with Diptera were not significant ($P > 0.05$; Supp Tables S1 and S4–S8 [online only]). At Cariblanco, there was a significant effect of date on damage associated with Hymenoptera ($P \leq 0.001$), but no significant effect of fruit maturity ($P = 0.291$), whereas at Vereh, the effects of date and fruit maturity on damage associated with Hymenoptera were not significant ($P > 0.05$; Supp Tables S1 and S4–S8 [online only]). Overall, even in the cases in which the correlation between herbivore damage and fruit maturity was statistically significant, the low correlation coefficient indicated that this correlation was weak (Supp Table 5 [online only]).

Impact of *M. luteofascia* on Seed Numbers and Seed Germination

Fruit damage by *M. luteofascia* larvae resulted in significantly lower numbers of seeds and lower germination rates ($P \leq 0.05$; Figs. 7 and 8; Supp S9 and S10 [online only]). Differences in number of seeds were significant between damaged and undamaged fruits ($P \leq 0.05$), but not between fruits with medium and high levels of damage ($P > 0.05$; Supp Table 9 [online only]). Germination was significantly lower in seeds from damaged compared with undamaged fruits ($P \leq 0.05$) and also in seeds from fruits with high damage compared with fruits with medium damage ($P \leq 0.05$; Supp Table 9 [online only]). For undamaged fruit, most seeds germinated in the interval between 40 and 90 d, with fewer seeds germinating earlier than 40 d and later

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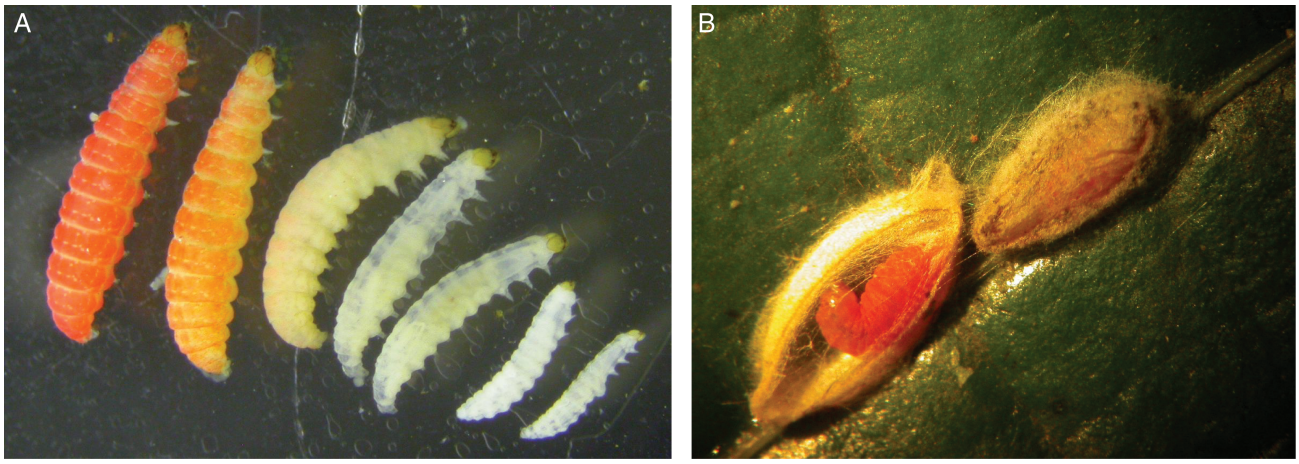

Fig. 5. Change in coloration of *Mompha luteofascia* larvae from early to late instars; from bottom right to top left the picture shows two first instars, two second instars, and three third instars (a). *Mompha luteofascia* pupa and larva spinning the cocoon to pupate (b). Photographs by M. A. Alfaro-Alpízar.

Table 1. Percentage of fruits damaged by *Mompha luteofascia* and other herbivores and percentage of damage per fruit (mean ± SE), among samples from two sites in Jan., Feb., and Mar. 2007

	Cariblanco (n = 4,192)		Vereh (n = 5,505)	
State of fruit	Fruits (%)	Damage per fruit (%)	Fruits (%)	Damage per fruit (%)
Mompha luteofascia larvae	13.05aA	42.27 ± 1.49aA	4.98bA	31.56 ± 1.85aADE
Other Lepidoptera	0.07[a]aB	8.33 ± 8.33aB	0.18aB	23.50 ± 9.22aCD
Coleoptera larvae	0.00[b]aC	0.00[b] ± 0.00a	2.09[c]bC	29.00 ± 3.04aBDEF
Diptera larvae	0.14aB	4.17 ± 0.83aB	1.16bD	1.59 ± 0.29aFBE
Hymenoptera larvae	0.14aB	8.33 ± 5.27aB	0.71bE	18.33 ± 1.88DAC
Unknown damage[c]	0.00[d]aC	2.50 ± 2.50aB	0.69bE	5.79 ± 2.43aE

Percentages within a row followed by different lower case letters, and within a column followed by different upper case letters, are significantly different ($P \leq 0.05$). A one-tailed two-sample test of proportions was used to compare the percentage of fruits damaged, and a Mann–Whitney U test was used to compare the percentage of damage per fruit in damaged fruit.

[a]Only three fruits affected.

[b]No insects present at the time of dissection.

[c]In Vereh, these corresponded to larvae of *Anthonomus monostigma*.

[d]Only two fruits with unknown damage in Cariblanco.

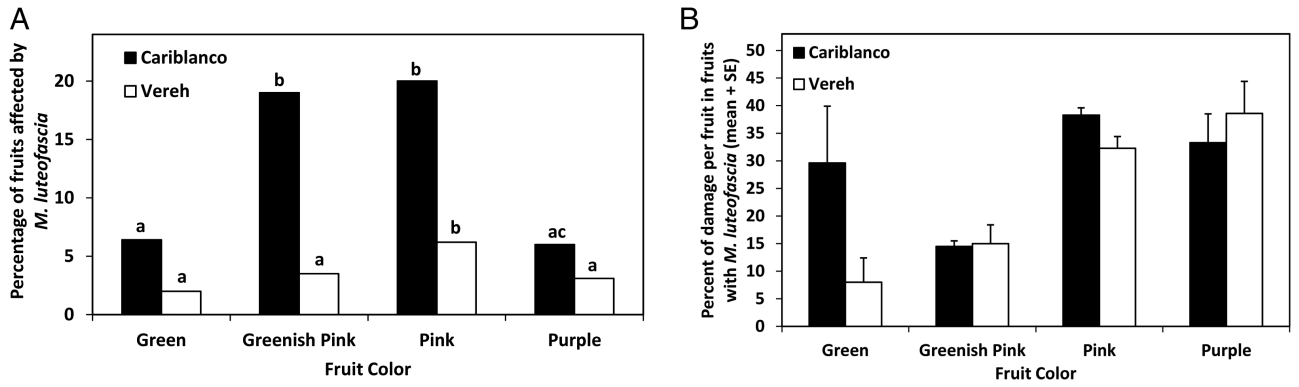

Fig. 6. Percentage of fruits damaged (a) and percent of damage per fruit (mean + SE) (b) in fruits of increasing maturity damaged by *Mompha luteofascia* at Cariblanco (n = 987; 12 green, 194 greenish pink, 744 pink, and 37 purple) and Vereh (n = 274; 5 green, 20 greenish pink, 206 pink, and 43 purple).

than 90 d ($P \leq 0.05$; Fig. 8; Supp Table 10 [online only]). There were no significant differences in the rates of germination at 60 and 90 d (P = 0.391; Supp Table 10 [online only]). For damaged fruit, there were no significant differences in time of emergence because germination was very low (Supp Table 10 [online only]).

Discussion

The new species *M. luteofascia* has a characteristic bent yellow fascia at one-third of its dark brown forewing. We determined that this species has three larval instars. To the best of our knowledge,

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the number of larval instars is unknown in other described species of Momphidae.

Among the herbivores that we found feeding in *M. calvescens* fruits, *M. luteofascia* shows great potential as a biological control agent. As a result of *M. luteofascia* feeding, seed germination was drastically reduced from 34.8% in undamaged fruits to 1.9 and 0.1% in fruits with medium and high fruit damage, respectively. Through impacts on reproduction of *M. calvescens*, *M. luteofascia* might prove a useful complement to the effects of a number of potential biological control agents under evaluation (Burckhardt et al. 2005; Badenes-Pérez and Johnson 2007a,b, 2008; Allen 2010; Badenes-Pérez et al. 2010, 2014; Hanson et al. 2010; Morais et al. 2010a,b, 2012, 2013; Nishida 2010; Reichert et al. 2010; Castillo et al. 2014).

The presence of *M. luteofascia* larvae in *M. calvescens* fruits was variable, reaching up to 38% of all the fruits sampled in Cariblanco in July 2006. At Vereh, *M. luteofascia* was less abundant than at Cariblanco. Damage caused by *M. luteofascia* at Vereh was complemented by damage caused by another frugivore, *A. monostigma*, which was not present at Cariblanco. Other insects found in *M. calvescens* fruits included Hymenopteran and Dipteran larvae, which were probably parasitic or commensal, respectively, with the two main insect frugivores. Our collections confirmed parasitism of *M. luteofascia* larvae by at least three hymenopteran species. Larvae of the hymenopteran *Allorhogas granivorus* Zaldívar-Riverón and Martínez have been found feeding in galled *M. calvescens* fruits in Brazil, but not in Costa Rica (Badenes-Pérez and Johnson 2007b, Zaldívar-Riverón et al. 2018). Feeding by *A. granivorus* results in an increased permanence of *M. calvescens* fruits in the tree (Badenes-Pérez and Johnson 2007b), whereas feeding by *A. monostigma* seems to produce early abscission of fruits (Chacón-Madrigal 2007). It is not clear if infestation by *M. luteofascia* affects fruit permanence in the tree.

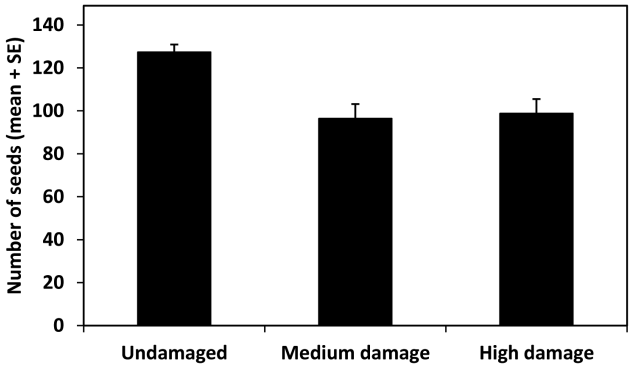

Fig. 7. Number of seeds in undamaged fruit and fruit with medium (50–75% pulp missing) and high damage (75–100% pulp missing) by *Mompha* sp. larvae (n = 63 for undamaged fruit, 5 for fruit with medium damage, and 12 for fruit with high damage).

Given the relatively high levels of parasitism of *M. luteofascia* in Costa Rica, this species might also suffer high parasitism if it were introduced to Hawaii, where the congeneric fruit-feeder *M. trithalama* is subject to parasitism in its host plant *Clidemia hirta* (Conant et al. 2013). In our study, despite high parasitism, the damage levels found in the field were still relatively high. In Hawaii, despite the parasitism, *M. trithalama* is well established, but its impact on *C. hirta* has not been quantified (Conant et al. 2013).

So far, the only known host plant of *M. luteofascia* is *M. calvescens*. Although this study did not evaluate the host range of *M. luteofascia*, there is a high likelihood that this herbivore is narrowly host specific given the known specificity of congeners, including some used in biological control of weeds, such as *M. trithalama* (Bradley et al. 1973, Nakahara et al. 1992, Conant 2002, Culliney et al. 2003). Our emphasis on first quantifying impact on the host plant, before conducting detailed host specificity testing, is consistent with the need to prioritize highly effective biocontrol agents and avoid expending limited resources for import and quarantine testing on species with low potential for meaningful control (McClay and Balciunas 2005, Johnson 2010).

The significant reduction of seed numbers and seed germination caused by larvae of *M. luteofascia* indicates that this species deserves further study to assess its potential as a biological control agent of *M. calvescens*. Seed feeders are sometimes considered useful

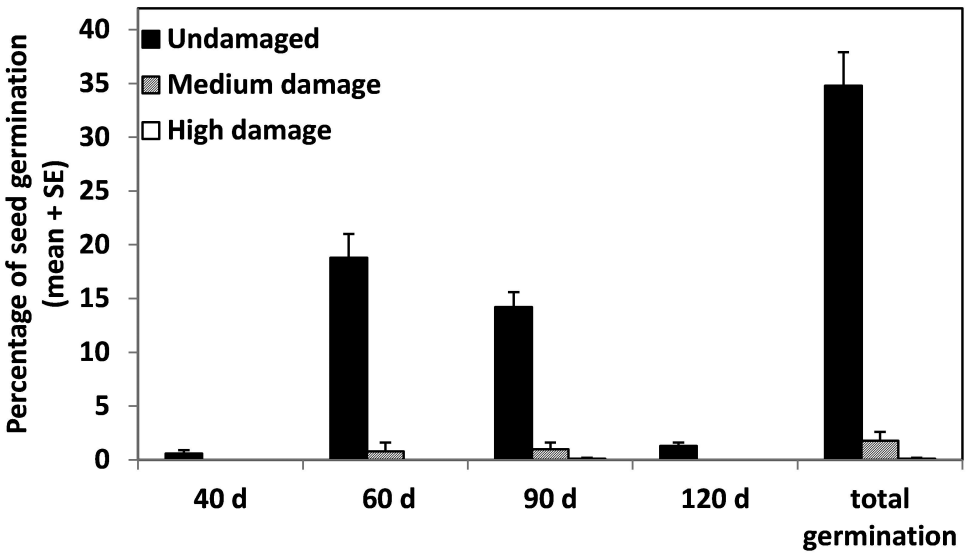

Fig. 8. Germination of seeds from undamaged fruit and fruit with medium (50–75% pulp missing) and high damage (75–100% pulp missing) by *Mompha luteofascia* larvae (n = 9,689 seeds from 80 fruits, from which 8,022 seeds were from undamaged fruits, 482 seeds were from fruits with medium damage, and 1,185 seeds were from fruits with high damage).

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biological control agents of weeds only in seed-limited plant systems (Myers 1978, Crawley 1992). Even if *M. calvescens* is not seed limited because it is dispersed by birds feeding on fruit (Spotswood et al. 2012, 2013), a measure of biological control success could be to reduce its spread as a result of reducing seed number and seed germination (Badenes-Pérez and Johnson 2007b). It would be helpful to better understand how perturbations of seed numbers and germination rates might affect *M. calvescens* population dynamics and dispersal potential, and whether infestation of *M. calvescens* fruit by *M. luteofascia* or other herbivores might affect fruit consumption by birds.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

Acknowledgments

We thank Paul Hanson, Edgar Rojas, Eduardo Chacón, and other members of the Proyecto Miconia team at the Universidad de Costa Rica for their assistance. Paul Hanson provided identifications of parasitoids. Erik van Nieukerken, Naturalis Biodiversity Center, Leiden, The Netherlands, is thanked for the correct Latin translation of the yellow band on the forewing of the species. Funding was provided by the Hawaii Invasive Species Council and USDA Forest Service International Programs.

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